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The earliest fully brachypterous auchenorrhynchan from Cretaceous Burmese amber (Homoptera: Fulgoroidea: Jubisentidae)

Древнейшая цикадка с сильно укороченными крыльями из мелового бирманского янтаря (Homoptera: Fulgoroidea: Jubisentidae)

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KEY WORDS: planthoppers, Perforissidae, wing dimorphism, brachyptery, sensory pits, phylogeny, fossil, host plants, grasses, camouflage, mimicry.

КЛЮЧЕВЫЕ СЛОВА: носатки, Perforissidae, крыловой диморфизм, короткокрылость, сенсорные ямки, филогения, ископаемые, кормовые растения, травы, маскировка, мимикрия.

ABSTRACT. *Psilargus anufrievi* **gen.** et **sp.n.** (Psilarginae **subfam.n.**) from mid-Cretaceous Burmese amber is assigned to the family Jubisentidae in basal (pre-cixioid) Fulgoroidea. The two formerly known genera of this family are placed in Jubisentinae **stat.n.** The only known specimen of the new species is a minute female with extremely shortened wings. It is the earliest recorded instance of extreme brachyptery in Auchenorrhyncha. All known Jubisentidae were flightless, camouflaged, and likely associated with herbs in the Burmese Cretaceous tropics.

РЕЗЮМЕ. *Psilargus anufrievi* **gen.** et **sp.n.** (Psilarginae **subfam.n.**) из среднемелового бирманского янтаря отнесён к семейству Jubisentidae среди примитивных (до-циксиоидных) Fulgoroidea. Два ранее известных рода этого семейства помещены в Jubisentinae **stat.n.** Единственный известный экземпляр нового вида — мелкая самка с сильно укороченными крыльями. Это древнейший отмеченный случай резкой короткокрылости у Auchenorrhyncha. Все известные Jubisentidae были нелетающими, обладали маскировкой и, вероятно, обитали на травах в бирманских меловых тропиках.

The mid-Cretaceous Burmese amber (ca. 100 Ma) is a real Aladdin's cave for paleoentomologists. This fossil resin was produced by araucarian trees in a rainforest [Poinar et al., 2007; Poinar, Buckley, 2008] on an island in the tropical Tethys Ocean between Gondwana and Laurasia [Westerweel et al., 2019], far from other Cretaceous Lagerstätten. Among many wonderful and unexpected insect taxa, three endemic planthopper families have recently been discovered in Burmese amber — Dorytocidae, Yetkhatidae and Jubisentidae [Emeljanov, Shcherbakov, 2018; Song et al., 2019; Zhang et al., 2019]. In the Burmese amber fauna these groups coexist with widespread Cretaceous families, such as Perforissidae [Shcherbakov, 2007a; Zhang et al., 2017] and Mimarachnidae [Shcherbakov, 2007b, 2017; Luo et al., 2020; etc.], and several extant families, such as Cixiidae and Achilidae [Shcherbakov, 2000; Szwedo, 2004] making up a rich and diverse planthopper assemblage [Perkovsky et al., 2019]. The latest find, recently offered on eBay, is an unusual brachypterous female planthopper described below as a new genus and subfamily of Jubisentidae.

The two Cretaceous planthopper families known from adults, Perforissidae and Mimarachnidae [Shcherbakov, 2007a, b] are referred to the basal, precixioid Fulgoroidea on account of having setigerous hind tibial pectens and the proximal CuA fork in the tegmen. The two other Cretaceous families based on nymphs with asetigerous hind tibial pectens, Neazoniidae [Szwedo, 2007] and Dorytocidae [Emeljanov, Shcherbakov, 2018] show other features in common with perforissids and mimarachnids. Subbrachypterous flightless Jubisentidae were described as related to Perforissidae [Zhang et al., 2019]. The new subfamily combines characters of typical jubisentids with a few perforissid characters and so bridges the gap between the two families.

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The holotype female of the new species is extremely brachypterous, with tegmina covering only the meso- and metanotum. Such advanced brachyptery is common in planthoppers (Delphacidae, Dictyopharidae Orgeriinae, Caliscelidae) and leafhoppers, as well as in some groups of true bugs [Schuh, Slater, 1995], occurs as a rare exception in froghoppers [Fennah, 1966], and is unknown in cicadas, treehoppers and Sternorrhyncha. Brachypterous leafhoppers and planthoppers have been reported from Eocene Baltic amber (Szwedo, 2002, fig. 24; Szwedo, Stroiński, 2013; Dietrich, Gonçalves, 2014), but appear to remain unknown from pre-Cenozoic strata. Therefore, the discovery of a strongly brachypterous planthopper in Cretaceous amber is of considerable interest. It seems to be the first record of a brachypterous Auchenorrhyncha from as far back as the Mesozoic.

In its general habitus, short veinless tegmina, and foliaceous fore and mid legs the new genus is similar to some Caliscelidae, especially *Caliscelis* de Laporte, 1833. Caliscelids sometimes show striking sexual dimorphism, with males mimicking jumping spiders [O'Brien, 1967] or ants [Gnezdilov, 2019]. Perforissidae also share many traits with Caliscelidae, though these two families are not closely related [Shcherbakov, 2007a].

Wing reduction occurs in Auchenorrhyncha feeding on herbs and forbs, but not in their arboreal relatives [Waloff, 1983]. Among grass feeding Auchenorrhyncha, flightless brachypterous forms are common in permanent habitats and rare in temporary ones [Denno et al., 1991; Novotný, 1994]. Caliscelidae and Delphacidae largely feed on grasses and often display wing dimorphism; the macropterous form can be very rare, for example, in Caliscelidae. The new species may be wing dimorphic as well. Its hypothetical macropterous form is expected to retain such diagnostic characters of the new subfamily as sensory pits, reduced setation, and modified head structure to be easily distinguishable from Jubisentinae, which are currently known by two subbrachypterous flightless species. Flightless Jubisentidae presumably fed on some herbaceous host plants, such as grass-like monocots of the Burmese amber flora [Poinar, 2004]. The new genus may be one of the earliest planthoppers associated with grasses, and its extreme brachyptery agrees with the assumption that some permanent grassy patches already existed in the mid-Cretaceous. Plants with vegetative morphology of grasses (*Graminophyllum*) are known since the Neocomian [Krassilov, 1982].

Nymphs of most planthopper families have sensory pits, forming rows and groups associated with carinae [Bräunig et al., 2012] and homologous to setigerous pits of Cicadomorpha [Emeljanov, 2001]. The sensory pits, supposed to be receptors of atmospheric humidity [Šulc, 1928], persist in adults of some planthopper taxa, especially in xerophiles or hygrophiles. The numerous sensory pits of adult perforissids suggest that they have lived in habitats with highly variable and/or extreme humidity [Shcherbakov, 2007a], like littoral environments with xeromorphic bennettite-brachyphyll communities, rich in proangiosperms and considered to have been the cradle of angiosperms [Krassilov, 1997]. The new genus of Jubisentidae, similar to perforissids in having numerous sensory pits, could also have inhabited herbaceous vegetation near the sea coast, on river banks, rocky outcrops, etc.

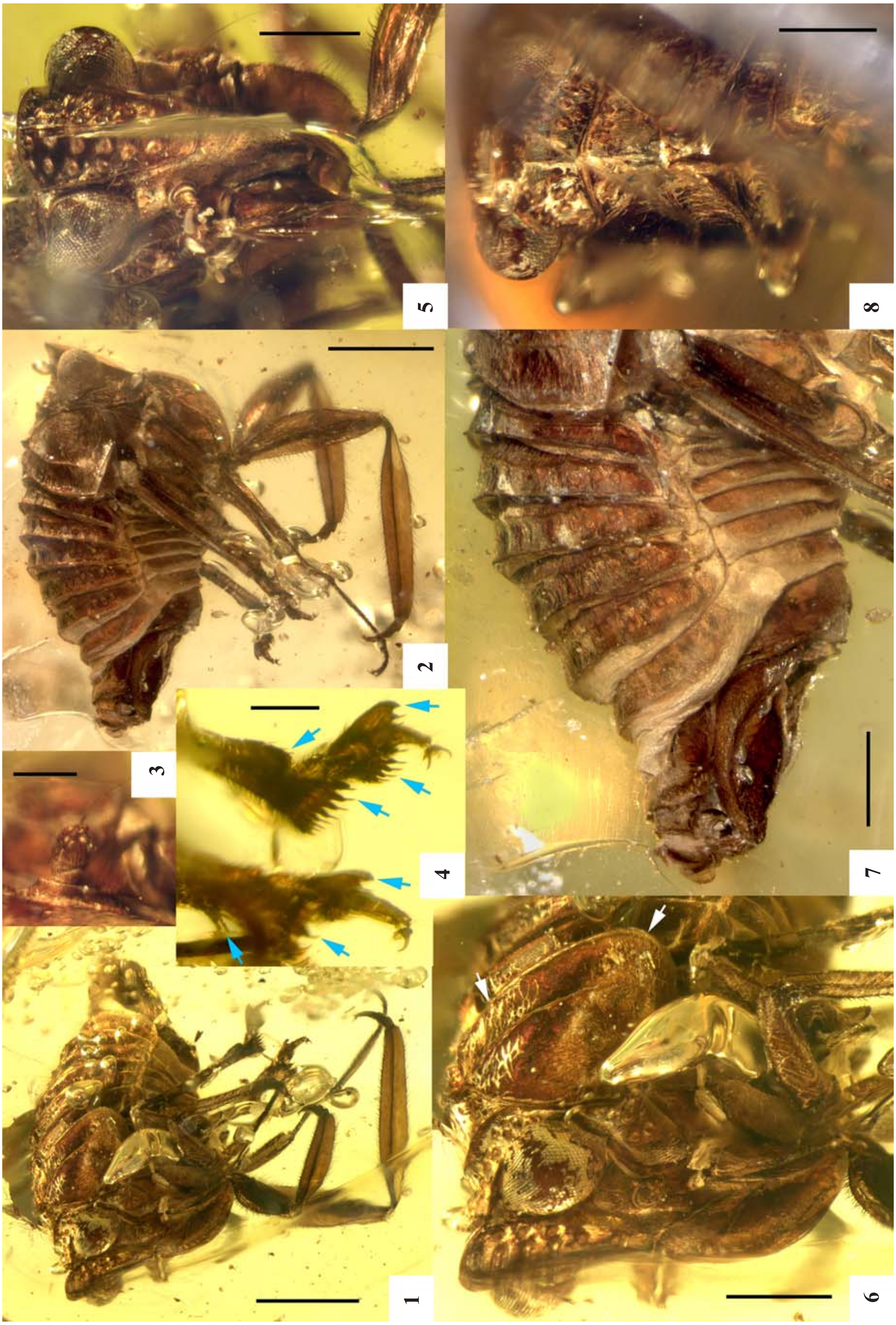
Various examples of camouflage and mimicry in insects from Burmese and other Cretaceous ambers indicate widespread occurrence of these phenomena in the Mesozoic tropics [Wang et al., 2016; Chen et al., 2019; Vršanský et al., 2019; etc.]. Some Mesozoic hoppers showing such camouflage elements as bizarre outgrowths, long head processes, foliaceous legs fringed with setae, or undulating margins of tegmina supposedly mimicked buds, strobiles or thorns of their host plants [Shcherbakov, 2011; Emeljanov, Shcherbakov, 2018], or adhered closely to the bark of host trees [Jiang et al., 2019]. Jubisentids also display elements of cryptic appearance [Zhang et al., 2019].

Some present-day hoppers, especially flightless, are masters of camouflage. Ground-dwelling subbrachypterous Myerslopiidae leafhoppers encrust their strangely shaped, ridged bodies with soil particles to blend into their environment [Rakitov, 2015]. Some brachypterous planthoppers, such as *Risius* Stål, 1859 (e.g. *R. gibbus* Fennah, 1967, *R. palamedes* Fennah, 1967, Fulgoridae) and *Kazerunia* Dlabola, 1974 (e.g. *K. leguaniforma* Dlabola, 1977, Tropiduchidae), have dorsal humps, ridges and lobes and resemble small lumps of dirt. The flattened and slender forms of Dorycephalini and Hecalini leafhoppers imitate grass seeds or twigs [Hamilton, 2000]. Brachypterous Orgeriinae planthoppers (Dictyopharidae) taking an unusual upright posture with their long legs stretched out [Ball, 1909] supposedly mimic the achenes of Asteraceae [Oshanin, 1913: 9] or salticid spiders [Emeljanov, 1980: 44]. The new apterous Burmese amber jubisentid appears camouflaged due to its serrated dorsal outline with transverse ridges, long foliaceous fore and mid legs fringed with setae, and brown colouration. On account of its long legs, it was likely mimicking spiders, seeds or plant debris rather than soil. A camouflage of this kind can be effective both on the host plant and near the ground.

The holotype of the new species is deposited at Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN). Photographs were taken using a Leica M165C stereomicroscope with a Leica DFC425 digital camera and z-stacked with Helicon Focus 7.0. Nomenclature of the planthopper cranium is given after Anufriev and Emeljanov [1988].

Family Jubisentidae Zhang et al., 2019

REVISED DIAGNOSIS. Small and compact planthoppers, at least legs with long setae. Eumetope and clypeus with median carina; clypeus strongly raised, without lateral carinae; rostrum extending beyond hind coxae, apical segment longer than wide. Ocelli absent. Pronotum with anterior margin produced beyond eye midlength, lateral margin posterior to eyes very short, posterior margin shallowly incised. Subbrachypterous or brachypterous, venation of tegmina


5
8
2
3
4
7
1
6

indistinct; tegula, claval suture and hind wing absent. Hind tibia without lateral teeth; all apical pectens of hind leg uniserial, of several teeth with subapical setae. Female abdomen short, ovipositor long, ensiform, its base about midlength of abdomen.

COMPOSITION. Two subfamilies.

Subfamily Jubisentinae Zhang et al., 2019, **stat.n.**

TYPE GENUS *Jubisentis* Zhang et al., 2019.

DIAGNOSIS. Body, legs and tegmina covered with long setae. Sensory pits absent at adult stage. Eumetope with median carina and weak submedian carinae, separated from coryphe by sandglass-shaped acrometope bordered with low carinae. Pronotum with median carina incomplete anteriorly; mesonotum without median carina. Subbrachypterous. Hind legs longest. Male pygophore elongate. Ovipositor projecting beyond anal tube.

COMPOSITION. Type genus and *Furtivirete* Zhang et al., 2019.

Subfamily Psilarginae Shcherbakov, **subfam.n.**

TYPE GENUS. *Psilargus* Shcherbakov, **gen.n.**

DIAGNOSIS. Legs with long setae, body bare. Sensory pits large, numerous at adult stage. Eumetope without submedian carinae, separated from coryphe by single high carina (no acrometope). Pronotum with median carina complete; mesonotum with median carina. Strongly brachypterous. Fore legs longest. Ovipositor not projecting beyond anal tube.

COMPOSITION. Type genus.

REMARKS. The new subfamily shows a few characters in common with Perforissidae — bare body with large sensory pits in adults, and eumetope without submedian carinae. However, this subfamily fits Jubisentidae in the other characters: clypeus with high median crest, shape of pronotum, foliaceous legs fringed with long setae, wing reduction and the absence of tegula, claval suture and ocelli. Jubisentinae also share one character with Perforissidae — the presence of the acrometope.

Psilargus Shcherbakov, **gen.n.**

TYPE SPECIES. *Psilargus anufrievi* Shcherbakov, **sp.n.**

DIAGNOSIS. Besides characters listed in subfamily diagnosis, differs from two known genera of nominate subfamily in the following features, mainly associated with brachyptery. Dorsal outline serrated in profile, with upcurved posterior edges of body segments and transverse ridges on tegmen and abdominal tergites. Lateral margins of pronotum exposed (overlapped by eyes reaching bases of tegmina in other jubisentid genera). Mesonotum triangular with apex truncate and upcurved (acute in other jubisentids). Fore legs longer than body (shorter). Hind tibiae slender with fin-like lateral lobe distally (foliaceous for entire length in other jubisentids). Subapical setae of hind leg pectens acuminate, of acutella type (slightly inflated, somewhat platella-like in other jubisentids); 2nd tarsal pecten with two outermost teeth asetigerous.

COMPOSITION. Type species.

ETYMOLOGY. From the Greek *psilos* (bare, smooth, naked), referring to the reduction of wings and body setae, and *Argos* (hundred-eyed guardian of Io), referring to dozens of round sensory pits; gender masculine.

Psilargus anufrievi Shcherbakov, **sp.n.**
Figs 1–8.

MATERIAL. Holotype brachypterous female PIN 5608/106 — Burmese amber, Hukawng Valley, Kachin State, Myanmar; mid-Cretaceous (Albian–Cenomanian).

DESCRIPTION. Body 3.6 mm long, compact, ovoid, somewhat compressed laterally, especially abdomen. Dorsal outline serrated in profile due to carina at head apex, raised or upcurved posterior edges of body segments, and transverse ridges on tegmina and abdominal tergites I–V. Dorsum without conspicuous longitudinal carinae or setae, finely longitudinally wrinkled, with one patch of transverse wrinkles in anterolateral part of tegmen. Head brown, dorsum unevenly suffused with brown, legs dark brown with pale spot under fore knee, sternites I–VI pale brown, sternite VII and ovipositor darker.

Head 1.3 mm wide, 1.9 mm high. Coryphe transverse, 3.5 times as wide as long, rising towards angulate anterior margin, with median carina. Eumetope 1.8 times as long as wide, gradually narrowed ventrally, twice as wide dorsally as ventrally, slightly tectiform in cross section, with median carina. Boundary of eumetope and coryphe arched in facial view, formed by single high carina faced dorsad. Each half of eumetope with about 15 sensory pits in two irregular rows, medial row of larger pits reaching level of antennae, lateral row of smaller pits restricted to dorsal half of eumetope. Clypeus as long as eumetope, with deeply arched median crest and oblique loroclypeal sutures not reaching it. Eyes large, ovoid. Antenna short, scape extremely short dorsally and slightly longer anteroventrally; pedicel ovoid, 1.5 as long as wide, with at least 12 sensory plaque organs. Rostrum 1.1 mm long, slender, reaching base of abdomen, with apical segment longer than wide.

Pronotum nearly 2.5 times as wide as long, with median carina; anterior margin trapezoidal, projecting forwards between eyes and somewhat overlapping coryphe; lateral margin very short, posterior margin W-shaped with shallow median incision; each half with nearly 15 sensory pits in two rows, anterior row of smaller pits and posterior row of larger pits with few smaller pits displaced posteriorly and forming rudimentary third row; pectoral lobe with 7 pits. Mesonotum subtriangular with apex truncate and upcurved, 1.7 times as long as wide, each half with 3 sensory pits anterolaterally; mesopleura small. Tegmina strongly brachypterous, truncate, wider than long, covering only thorax (abdominal tergite I free), not meeting with their commissural margins, without traces of veins, with narrow epipleuron separated by lateral carina, and transverse posterior submarginal ridge aligned with apex of mesonotum; metapleura large, anepisternum very dark, convex.

Coxae, femora and tibiae fringed along ribs with dark, erect, long and shorter setae. Coxae long, fore and mid coxae

Figs 1–8. *Psilargus anufrievi* **gen.** et **sp.n.,** holotype female, Burmese amber: 1 — habitus, anterolateral view; 2 — habitus, lateral view; 3 — antenna, anterior view; 4 — distal parts of hind legs (arrows — tibial lobe and apical pectens); 5 — head, frontal view; 6 — head and thorax, anterolateral view (arrows — margin of tegmen); 7 — abdomen, lateral view; 8 — head and thorax, dorsal view. Scale bars: 1–2 — 1 mm; 3–4 — 0.2 mm; 5–8 — 0.5 mm.

Рис. 1–8. *Psilargus anufrievi* **gen.** et **sp.n.,** голотип, самка, бирманский янтарь: 1 — общий вид, спереди-сбоку; 2 — общий вид, сбоку; 3 — антенна, спереди; 4 — вершины задних ног (стрелки — лопасть на голени и гребни); 5 — голова, спереди; 6 — голова и грудь, спереди-сбоку (стрелки — край элитры); 7 — брюшко, сбоку; 8 — голова и грудь, сверху. Длина масштабной линейки: 1–2 — 1 мм; 3–4 — 0,2 мм; 5–8 — 0,5 мм.

about as long as thorax height above them; fore coxae with outer edge foliaceous. Fore legs 3.8 mm long. Fore femora and tibiae foliaceous with outer margin more convex than inner margin; tarsi of subequal segments, 1st segment flattened laterally and highest, 3rd slender and longest. Mid legs 2.6 mm long, slender, femora flattened, tibiae narrow foliaceous, tarsi slender with 3rd segment longest. Hind legs 3.4 mm long. Hind trochanter largely membranous, with dark hook-like sclerotization along anteroventral side. Hind tibia quadrilateral, slightly curved, twisted distally, without lateral teeth, with fin-like lateral lobe on posterodorsal rib subapically. Apices of hind tibia and 1–2nd tarsomeres swallow-tailed with apical pectens of numerous setigerous teeth. Tibial pecten arched in apical view, all 8 teeth with long subapical setae. 1st tarsomere longest with pecten semicircular in apical view, of 10 teeth, outermost teeth with shortened subapical setae. 2nd tarsomere shortest, compressed laterally, inserted into 1st, with pecten deeply V-shaped in apical and dorsal views, of 14 teeth, both outermost teeth widened, without subapical setae. 3rd tarsomere slender. Claws simple, slender, strongly curved and tapered to apices; arolium well developed, wide, much shorter than claws.

Abdomen 2.6 mm long, tergites and sternites deeply arched or almost V-shaped. Tergites I–VI short with raised posterior margin, I–V also with anterior submarginal ridge and in each half with 1(2) submedian sensory pit and lateral row of several pits (I — 1, II — 4, III — 5, IV — 6, V — 3); tergite VI without pits. Spiracles visible as dark dots on membranous laterotergites near anterolateral angles of tergites I–V; laterotergite VI without spiracle, not separated from sternite. Sternites I–VI shorter than tergites. Tergites VII–VIII apparently somewhat reduced and/or hidden between membranous folds; sternite VII much longer, more convex and sclerotized than preceding, with shallow submedian posterior incisions. Segment IX (pygophore) elongate, tapered caudally, with anterior margin deeply incised, posterior submarginal ridge and lateral row of 5 sensory pits beyond it; ventral side concave, housing ovipositor. Ovipositor well developed, 1.2 mm long, occupying half of abdomen length. 3rd valvulae broad, lancet-shaped, consisting of outer subcylindrical rachis downcurved and tapered to acutely rounded apex, and lip-like blades with arched edges directed ventromedially, meeting along midline and leaving only bases of cutting inner valvulae exposed. Segment X (anal tube) as long as wide; dorsal side roof-shaped with median carina; lateral carinae with rectangular acuminate posterior angles; apical side with paired drop-shaped epiprocts and short anal style.

ETYMOLOGY. The species is dedicated to the memory of a Russian expert in Auchenorrhyncha, Georgy A. Anufriev (1943–2017).

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